

Visual symmetry in objects and gaps

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It is known that perceptual organization modulates the salience of visual symmetry. Reflectional symmetry is more quickly detected when it is a property of a single object than when it is formed by a gap between two objects. Translational symmetry shows the reverse effect, being more quickly detected when it is a gap between objects. We investigated the neural correlates of this interaction. Electroencephalographic data was recorded from 40 participants who were presented with reflected and translated contours in one- or two-object displays. Half of the participants discriminated regularity, half distinguished number of objects. An event-related potential known as the Sustained Posterior Negativity (SPN) distinguished between reflection and translation. A similar ERP distinguished between one and two object presentations, but these waves summed with the SPN, rather than altering it. All stimuli produced desynchronization of 8–13 Hz alpha oscillations over the bilateral parietal cortex. In the Discriminate Regularity group, this effect was right lateralized. The SPN and alpha desynchronization index different stages of visual symmetry discrimination. However, neither component displayed the Regularity \times Objecthood interaction that is observed in speeded discrimination tasks, suggesting that integration of visual regularity with objectness is not inevitable. Instead, both attributes may be processed in parallel and independently.

Introduction

The visual system is extremely sensitive to symmetry. This could be because symmetry indicates the presence of objects, because it facilitates figure-ground segregation in a visual scene, or because it is a cue indicating mate quality (see Treder, 2010; Tyler, 1995; Wagemans, 1995, for reviews). Symmetry perception can be demonstrated in newly-hatched poultry chicks (Mascalzoni, Osorio, Regolin, & Vallortigara, 2012), and bees can discriminate symmetry in flowers (Plowright, Evans, Leung, & Collin, 2011). Reflectional symmetry, rotational symmetry, and translation are equally regular in terms of the number of isometric transformations involved (Mach, 1886/1959). However, numerous psychophysical studies have shown that reflection is the most efficiently detected (Makin, Pecchinenda & Bertamini, 2012a; Palmer & Hemenway, 1978; Royer, 1981).

Two-dimensional retinal images can be produced from an infinite number of different three-dimensional objects. In addition, there are an infinite number of ways to parse surfaces and edges, but only a subset of groupings allow people to reliably perceive whole objects. For these reasons, it is necessary to impose prior constraints on perceptual interpretation (e.g., Pizlo & Stevenson, 1999). The fact that objects often have reflectional symmetry could help the visual system get a handle on the inverse problem, perhaps explaining why humans are especially sensitive to reflection. This

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view, therefore, suggests a close link between reflectional symmetry and objecthood (Treder & van der Helm, 2007). However, the statistical association between symmetry and whole objects may only hold for biological organisms and human products (Tyler, 1995), and we have little difficulty with recognizing asymmetrical objects like rocks. The connections between symmetry and objecthood are thus controversial, and require further study.

We therefore focused on the relationship between reflectional symmetry and objectness. We compared electrophysiological responses to patterns where reflectional symmetry was either congruent or incongruent with other cues indicating the presence of a single object. Specifically, reflectional symmetry may produce different electroencephalographic (EEG) activity when it is the property of a single object than when it is formed by a ground region between two objects. This would support the idea that visual sensitivity to reflection has emerged because of its role in object representation.

There have been several excellent neuroimaging studies on symmetry perception. First, Tyler et al. (2005) measured cerebral blood flow with functional magnetic resonance imaging (fMRI) while people viewed reflection or random images. It was found that the lateral occipital complex (LOC), but not V1 or V2, was more active when people viewed symmetry (see also Chen, Kao, & Tyler, 2007; Sasaki, Vanduffel, Knutsen, Tyler, & Tootell, 2005). These results are corroborated by evidence that transcranial magnetic stimulation (TMS) disruption to the LOC, but not V1, alters symmetry discrimination (Cattaneo, Mattavelli, Papagno, Herbert, & Silvanto, 2011).

EEG has also been profitably employed to explore symmetry perception. Norcia, Candy, Pettet, Vildavski, and Tyler (2002) measured event-related potentials (ERPs) produced by sequences of reflection and random patterns. The waveform for reflection became relatively more negative from around 220 ms onwards. Jacobsen and Höfel (2003) also recorded ERPs while people viewed regular or random patterns. In some conditions participants categorized the patterns as symmetry or random; on other conditions they evaluated the patterns as beautiful or ugly. In all tasks, symmetry produced lower amplitude wave than random patterns from around 600 ms to the 1100 ms poststimulus onset. This difference wave was termed the Sustained Posterior Negativity (SPN). The SPN was reduced, but not eliminated, when participants made aesthetic judgments. In subsequent studies, the SPN was found when people performed oddball detection task rather than symmetry discrimination (Höfel & Jacobsen, 2007a), or when people deliberately misreported their responses (Höfel & Jacobsen, 2007b).

In a more recent EEG study, Makin, Wilton, Pecchinenda, and Bertamini (2012) again presented reflection and random patterns. The SPN was not influenced by whether reflection or random required a “Yes” or “No” response, although EMG activity recorded from facial muscles was reversed by this manipulation. Another study from our lab recorded SPN for reflection, translation, rotation, and random patterns (Makin, Rampone, Pecchinenda, & Bertamini, 2013). It was found that the SPN was most pronounced for reflection, but was still present for rotation and translation. SPN amplitude thus maps the ordinal sequence of visual salience for different regularities.

Makin, Wilton, et al. (2012) also explored their EEG data in a different way. They measured changes in alpha oscillations (defined as 10–14 Hz in that report) while participants discriminated reflection and random patterns. Alpha power was reduced at posterior electrode clusters around 400 ms after stimulus onset. Event-related desynchronization (ERD) in the alpha band is assumed by several models to reflect activation of task relevant networks, enacted by a shift from default slow wave oscillations to task specific, higher frequency communication (Buzsáki, 2006; Klimesch, Sauseng, & Hanslmayr, 2007; Pfurtscheller & Lopes da Silva, 1999). Makin, Wilton et al. (2012) found that Alpha ERD was more pronounced over the right hemisphere, indicating that the right hemisphere was more active than the left during regularity discrimination. This lateralization is interesting, because the right hemisphere is specialized for visuospatial global operations (Bradshaw & Nettleton, 1981). For example, damage to the right hemisphere causes pronounced difficulties in orientating spatial attention (Mesulam, 2002), and the right superior parietal lobule is crucially involved in mental object rotation (Parsons, 2003). Makin, Wilton, et al. (2012) speculated that symmetry discrimination might recruit these right hemisphere attentional networks, resulting in right lateralized ERD (cf. Verma, Van der Haegen, & Brysbaert, 2013). However, we now note that the occipital alpha rhythm is not likely to result *directly* from alpha in the frontoparietal attentional network, but is probably produced by recurrent loops connecting the thalamus to early visual areas (Buzsáki, 2006), so many questions remain.

The neuroimaging work to date has measured brain responses to symmetrical objects or patterns; however, it has not directly addressed the putative importance of symmetry in figure-ground segmentation. Indeed, symmetry need *not* be the property of a figure; it is possible to have a *symmetrical gap* between two objects. Examples of symmetrical objects and gaps are shown in Figure 1. Unlike the neuroimaging literature, many psychophysical studies have measured the relative salience of these stimulus types. A common finding is

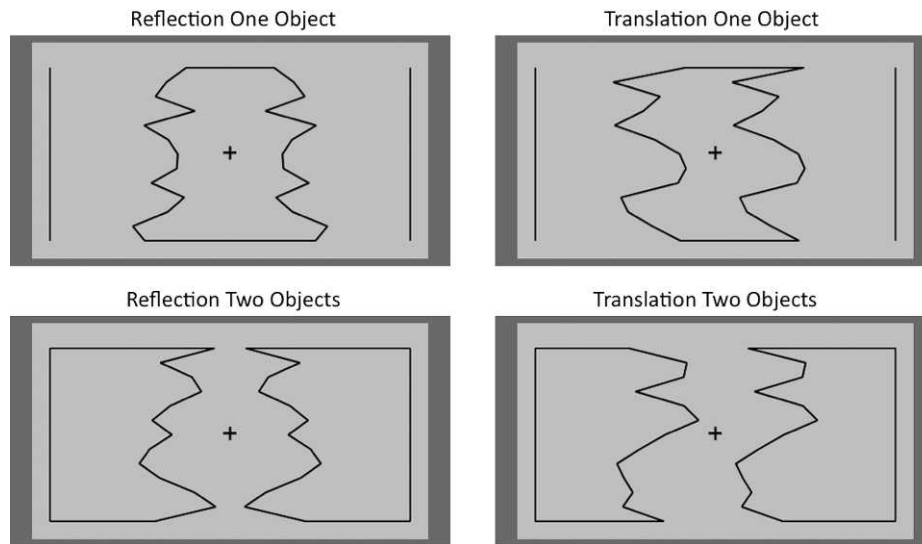


Figure 1. Example stimuli from the four conditions. Novel patterns were generated on each trial, so no image was presented twice to an observer.

that reflectional symmetry is more quickly perceived when it is the property of a single object than a gap, but this one object advantage can be reversed for translation (Baylis & Driver, 1995; Bertamini, Friedenber, & Argyle, 2002; Bertamini, Friedenber, & Kubovy, 1997; Corballis & Roldan, 1974; Koning & Wagemans, 2009; Makin, Pecchinenda, & Bertamini, 2012b; Treder & van der Helm, 2007).

We were interested in whether the SPN or right hemisphere alpha ERD would be fundamentally altered by the figure-ground status of symmetrical patterns. We presented patterns like those shown in Figure 1 and predicted that the SPN would distinguish between reflection and translation, as found by Makin et al. (2013). One possibility is that the SPN might be reduced or even reversed when regularity is represented by a gap between two objects, in line with the findings of speeded discrimination tasks. If this is the case, we can conclude that networks that generate the SPN produce this regularity \times objecthood interaction. The same reasoning applies to the right-sided alpha ERD: If this signal demonstrated regularity by objecthood interaction, it would likely arise from the brain regions responsible for the equivalent interaction in speed discrimination tasks.

We were also interested in the N1 component, because previous research has shown effects of symmetry, perceptual organization, and shape processing at this latency. Regarding symmetry, Makin, Wilton, et al. (2012) found larger N1 for reflection than random patterns, while Makin et al. (2013) found a larger N1 for reflection than translation. An N1 effect was not reported in previous research on symmetry ERPs (Höfel & Jacobsen, 2007a; Jacobsen & Höfel, 2003) possibly because the regular/random stimuli

appeared at the same time as a large high contrast background in those studies. Regarding perceptual organization, Machilsen, Novitskiy, Vancleef, and Wagemans (2011) found that the enhancement of the N1 in the presence of a contour was larger for iso-oriented than for randomly-oriented backgrounds, with the N1 being the only analyzed component showing an interaction between contour integration and the context it was presented in. Therefore, we also analyzed the N1 component to assess if regularity by objecthood interactions might emerge at this stage.

Another important comparison in our experiment was between a group of participants actively involved in regularity discrimination (Reflection or Translation) and another group who was presented with the same stimulus, but discriminated the number of objects (One or Two). Any electrophysiological measures that are purely related to stimulus characteristics should be similar in both groups. Conversely, any effect uniquely related to active symmetry discrimination should be found in the Discriminate Regularity group only.

Method

Participants

Forty participants were involved in this study (age 17 to 55, three left handed, 17 male). All participants had normal or corrected-to-normal vision, and were reimbursed £10 or awarded course credits. The study had

local ethics committee approval and was conducted in accordance with the Declaration of Helsinki.

Apparatus

The apparatus was the same as that used in Makin, Wilton, et al. (2012) and Makin et al. (2013). Participants sat in an electrically shielded and darkened room. The stimuli were presented on a 40 × 30 cm, 60 Hz CRT monitor (Mitsubishi, Tokyo, Japan) approximately 140 cm from the participants. The experiment was generated using *PsychoPy* (Peirce, 2007). EEG data were recorded continuously from 64 scalp electrodes arranged according to the international 10–20 system, using a BioSemi active-two amplifier sampling at 512 Hz (BioSemi, Amsterdam, Netherlands). Two additional electrodes, the Common Mode Sense (CMS) and Driven Right Leg (DRL) were used as reference and ground. Four external electrodes were used to record the horizontal and vertical electro-oculograph (EOG).

Design

Participants viewed four different types of stimuli, produced by crossing two factors: Regularity (Reflection, Translation) and Objecthood (One object, Gap between two objects). Twenty participants discriminated regularity, ignoring the number of objects. Another 20 participants discriminated the number of objects, ignoring regularity.

Stimuli

Example stimuli are shown in Figure 1. Novel patterns were generated on each trial, so no image was presented twice across the entire group of 40 participants. On each trial, a vertical contour was generated using a random-walk algorithm with 12 inward and outward turns. The maximum and minimum displacement from the reference line was $\pm 0.64^\circ$. These vertices were equally spaced by 0.21° on the *Y*-axis, so contour height was approximately 2.56° . The resulting contour was then translated or reflected across the midline. The horizontal distance from reference to the midline was 0.85° of visual angle.

The two jagged lines (reflected or translated) were not presented in isolation. Instead they were embedded in a context that closed the lines to form either a single central shape, or two opposite shapes.

The overall width of the stimuli was 5.11° , as defined by the two vertical lines on the outside. Horizontal lines at the top and bottom defined whether the patterns

constituted one object (lines meeting in the middle) or two objects (lines connecting the contours to the outside edges). Stimuli were presented for 2 s, following a randomized 1.5- to 2-s baseline. A central fixation cross was present throughout the baseline and stimulus presentation period, and participants were encouraged to fixate and avoid blinking during this period.

Procedure

On each trial, participants observed a pattern, either reflection or translation, comprised of one object or the gap between two objects. There were 72 repeats of each condition, giving 288 trials in total. After the pattern disappeared, participants were prompted to enter their judgments. For the Discriminate Regularity group the task was to press one button for reflection and another for translation. For the Discriminate Number group the task was to press one button for one object and another for two objects. Participants pressed the A button with their left hand and the L button with their right hand. The response mapping was indicated by the position of words on the response screen. For example, in the Discriminate Regularity group, participants would see the words “REFLECTION” and “TRANSLATION” on the left and right of the midline. The position of the words was unpredictable on each trial, and indicated the meaning of the left (A) and right (L) buttons on the computer keyboard. For the Discriminate Number group, the words “ONE” and “TWO” were used in the same way. This design prevented preparation of motor readiness potentials during the period when the patterns were on the screen (Makin, Poliakoff, Ackerley, & El-Deredy, 2012).

ERP analysis

EEG signals from the 64 scalp electrodes were analyzed offline using the EEGLAB toolbox for Matlab (Delorme & Makeig, 2004). Data was re-referenced to a scalp average and low-pass filtered at 40 Hz. We then downsampled to 128 Hz to reduce file size and extracted epochs from -1 to 2 s, with a -200 to 0 ms baseline. Eye movement, blink, and other gross artefacts were removed from the epochs using independent components analysis (ICA; Jung et al., 2000). Data was reformed as 64 independent components and an average of 11.25 components were removed from each participant’s data (minimum = 2, maximum = 21). The number of excluded components was comparable in the Discriminate Regularity and Discriminate Number groups (11.5 vs. 11.0, $t(38) < 1$, n.s.). After ICA, we removed epochs with amplitude exceeding \pm

100 μV . Approximately 9% of the trials were removed from each condition; again there were no differences between conditions, $F(3, 117) < 1$, n.s., and no difference between Discriminate Number and Discriminate Regularity groups, $F(1, 38) < 1$, n.s. Finally, trials from the same condition were averaged within participants' data sets.

The SPN was defined as the difference between reflection and translation waves from 250 to 1000 ms poststimulus. We first ran a series of t tests on the combined wave from the PO7 and PO8 electrodes to empirically determine when the SPN began. The first significant difference between reflection and translation ERPs was 250 ms ($p < 0.05$). This latency is in close agreement with previous work (e.g., Norcia et al., 2002). Supplementary analysis based on different electrode clusters and time windows leads to the same conclusions. N1 was defined as amplitude from 160 to 220 ms at the same electrodes. Statistical analysis was done with a mixed analysis of variance (ANCOVA). There were two within-subjects factors (Regularity [Reflection, Translation] \times Objecthood [One object, Two objects with a gap]) and one between-subjects factor (Task [Discriminate Regularity, Discriminate Number]). With all ANOVA analyses reported below, the Greenhouse-Geisser correction factor was used when the assumption of sphericity of error variance was violated (Greenhouse & Geisser, 1959).

Time-frequency analysis

Time-frequency analysis was performed on the same cleaned EEG data using the FieldTrip toolbox for Matlab (Oostenveld, Fries, Maris, & Schoffelen, 2011). We focused on frequencies from 5 to 20 Hz in 1 Hz increments. EEG data was convolved with a variable length Hanning-tapered wavelet comprising four complete cycles at each frequency. Times of interest were set as -500 to 1500 ms. We then baseline-corrected the frequency data with reference to a -500 to 0 ms baseline. Power was calculated as a proportion of change in power relative to the baseline interval.

The analysis identified substantial desynchronization in the 8 to 13 Hz frequency band, from around 400 ms onwards in posterior electrode clusters (PO7, PO3, P1, P3, P5, P7, P9, CP1, CP3, CP5, and right-sided homologues). Power was analyzed as a function of 3 within-subjects factors (Hemisphere [Left, Right] \times Regularity, [Reflection, Translation] \times Objecthood [One object, Two objects with a gap]), and one between-subjects factor (Task [Discriminate Number, Discriminate Regularity]) with a mixed ANOVA.

EOG analysis

In this experiment participants were instructed to fixate on a central cross during the baseline and stimulus intervals. In order to establish that unwanted eye movements and blinks were evenly distributed across conditions, we measured activity in the horizontal and vertical EOG electrodes. We extracted -500 to 1500 ms epochs, with -200 to 0 ms baseline. For this analysis we did not exclude any trials, or perform any artefact correction procedures. For each subject and condition we calculated absolute amplitude (ignoring the sign) across each epoch, then we averaged over epochs. There was no difference in VEOG activity between the four conditions, $F(1.27, 49.39) = 1.498$, $p = 0.232$, or between Discriminate Regularity and Discriminate Number groups, $F(1,38) < 1$, n.s. Likewise, HEOG activity was equally distributed across the four conditions, $F(3, 114) < 1$ n.s., and between Discriminate Regularity and Discriminate Number groups, $F(1, 38) < 1$, n.s. This analysis indicates that any observed ERP and ERD effects are not attributable to eye movement artefacts, or represent a side effect of artefact correction procedures.

Results

Behavioral data

Participants could perform the tasks. In the Discriminate Regularity group, the mean percentage of correct judgments in each condition was as follows: reflection of one object (93%), reflection of two objects (94%) translation of one object (94%), translation of two objects (93%). In the Discriminate Number group, the mean percentage of correct judgments was 97% in all conditions.

N1

Grand average ERPs from the PO7 and PO8 electrodes are shown in Figure 2. It can be seen that the N1 potential was similar in reflection and translation trials (panel B), but greater for two-object trials than one-object trials (panel C).

This was confirmed with mixed ANOVA. There was no main effect of Regularity, $F(1, 38) < 1$, n.s., and although there was a Regularity \times Task interaction, $F(1, 38) = 6.708$, $p = 0.014$, partial $\eta^2 = 0.150$, the effect of Regularity did not reach significance when the tasks were analyzed separately (Discriminate Regularity [$F(1, 19) = 4.037$, $p = 0.059$]; Discriminate Number [$F(1, 19) = 3.055$, $p = 0.097$]). There was a very strong main effect

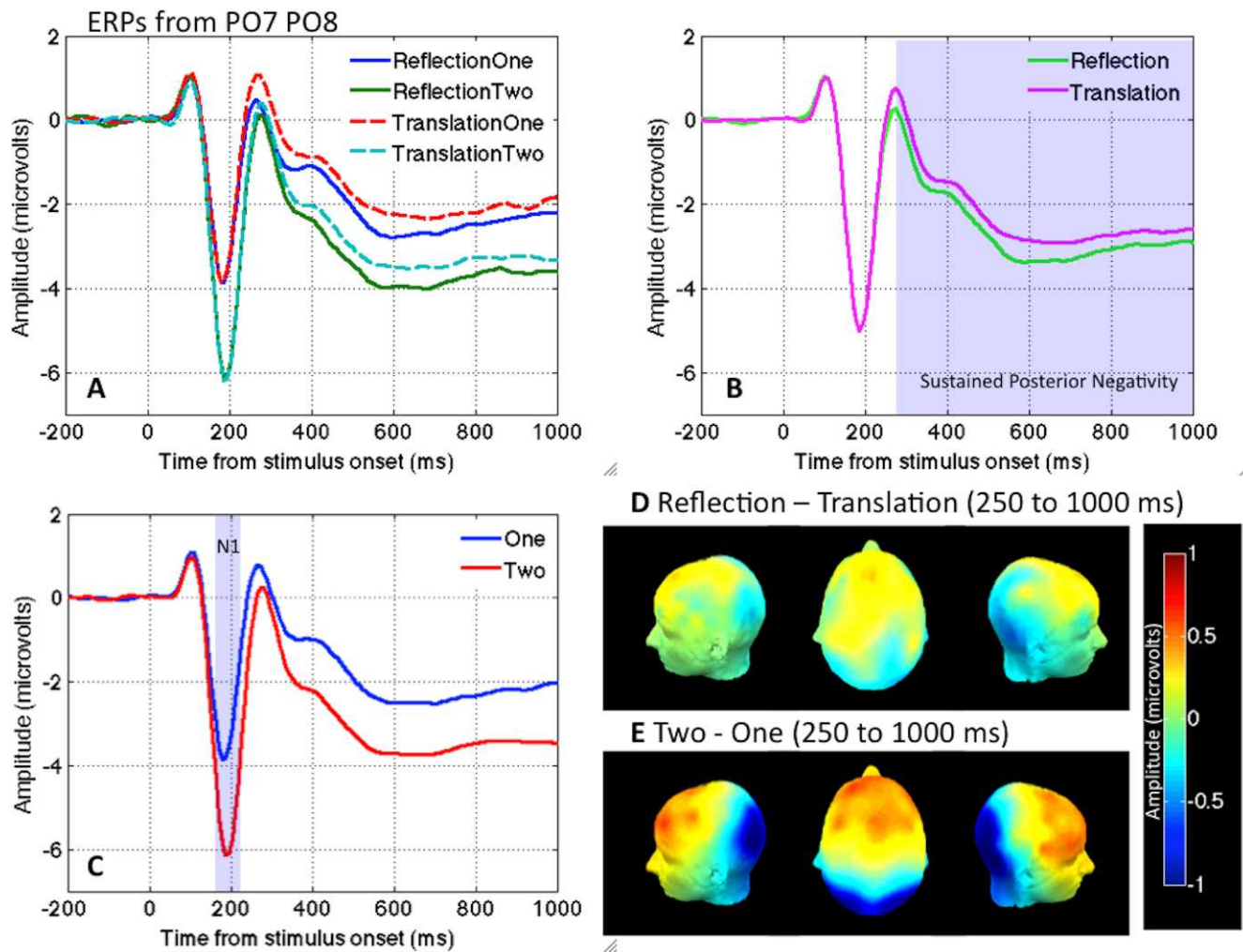


Figure 2. ERP results. (A) Grand Average waveforms recorded from PO7 and PO8 electrodes in all conditions. (B) ERPs in the reflection and translation trials (collapsed across Number). (C) ERPs from the one- and two-object trials (collapsed across Regularity). Waves have been smoothed with a 10-point moving average filter. (D) and (E) Topographic difference plot from the 250- to 1000-ms time window. Blue = higher amplitude in the translation than reflection trials (D), and higher amplitude in the one-object than two-object trials (E). The same scalp plots are shown from three angles. All data shown here is averaged across Task.

of Objecthood, $F(1, 38) = 81.194$, $p < 0.001$, partial $\eta^2 = 0.681$, that was not further modulated by Task, $F(1, 38) < 1$, n.s.). Crucially, there was no Regularity \times Objecthood interaction, $F(1, 38) < 1$, n.s., no three-way interaction between Regularity, Objecthood, and Task, $F(1, 38) < 1$, n.s., and no main effect of Task, $F(1, 38) = 1.019$, $p = 0.319$.

Sustained posterior negativity

The sustained posterior negativity was defined as amplitude between 250 and 1000 ms poststimulus onset. Figure 2A shows amplitude in all four conditions. It can be seen that the amplitude is sensitive to regularity (as expected) and also to objecthood, with

higher amplitude in the one object condition than the two objects with gap conditions.

The difference between Reflection and Translation waves replicates the results of Makin et al. (2013). The difference between one- and two-object presentations was much larger than the SPN (Figure 2C), but with a similar topography (Figure 2E). Although we predicted a Regularity \times Objecthood interaction, this was not apparent from the waveforms (Figure 2A).

SPN amplitude was explored with a mixed ANOVA. The main effect of Regularity was significant, $F(1, 38) = 6.035$, $p = 0.019$, partial $\eta^2 = 0.137$, because amplitude was lower in the reflection trials than the translation trials (Figure 2B). This effect did not interact with the between-subjects factor Task, $F(1, 38) < 1$, n.s., indicating that the SPN was comparable whether people were discriminating regularity or number. The main effect of Objecthood was significant, $F(1, 38) =$

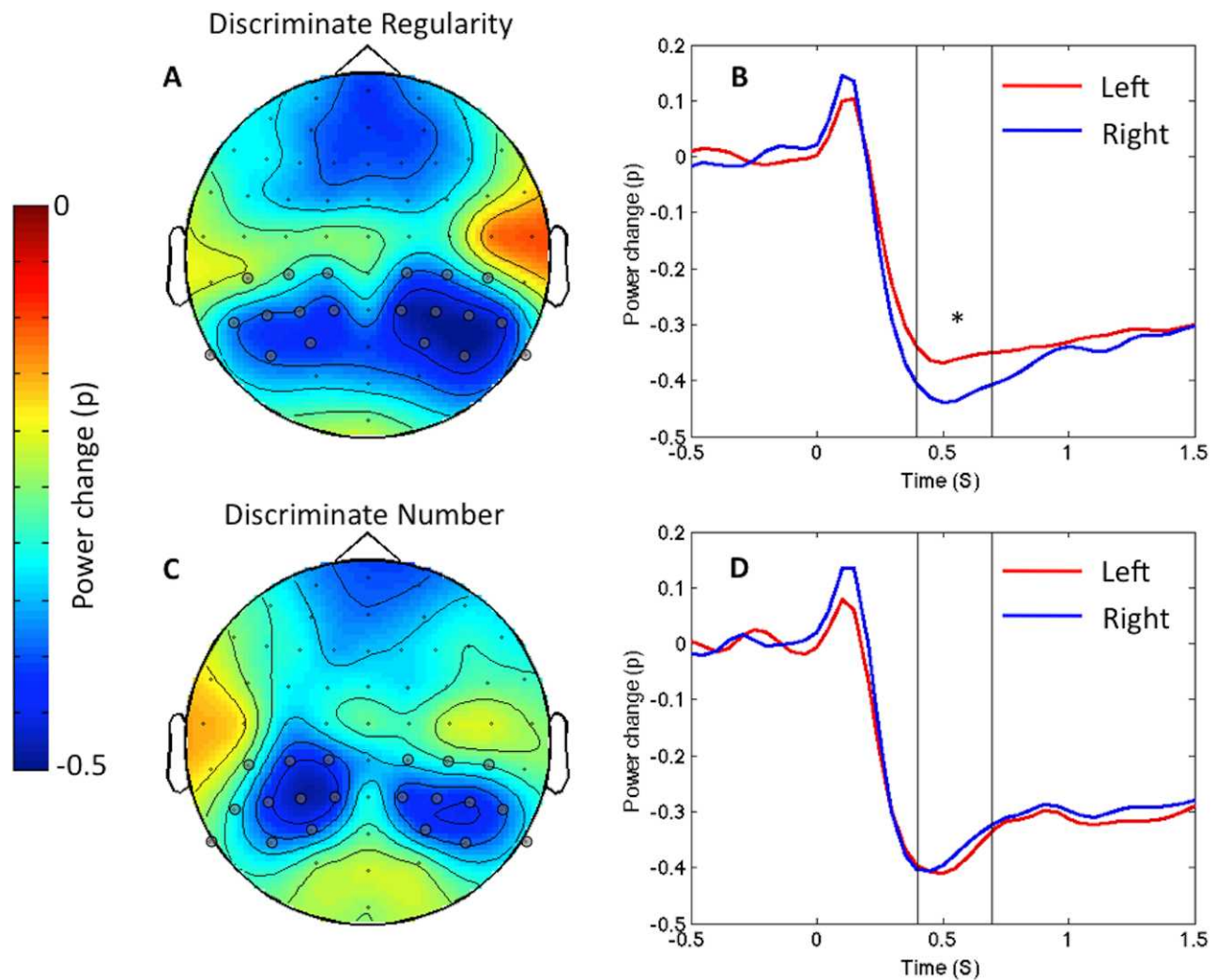


Figure 3. Alpha desynchronization in each task. Data from the Discriminate Regularity task is shown in the upper panels (A) and (B), data from Discriminate Number task is shown in lower panels (C) and (D). The gray disks in (A) highlight the position of the electrodes used in all analysis. Topographic plots show the reduction in alpha power (8–13 Hz) as a proportion of power during baseline. This averages over the 400- to 700-ms time window, and over regularity and number conditions. The right panels show ERD as a function of time in the left and right posterior electrode clusters. Note the lateralization in the Discriminate Regularity task, but not in the Discriminate Number task.

36.503, $p < 0.001$, partial $\eta^2 = 0.490$, Figure 2C, which did not interact with Task, $F(1, 38) < 1$, n.s. Most importantly, there was no Regularity \times Objecthood interaction, $F(1, 38) < 1$, n.s., and no three-way interaction between Regularity, Objecthood, and Task, $F(1, 38) < 1$, n.s.. Finally, the main effect of Task was not significant, $F(1, 38) = 2.006$, $p = 0.165$.

Alpha desynchronization

Patterns of posterior alpha desynchronization are shown in Figure 3. Unlike the ERPs, ERD showed important differences between the groups of participants performing Discriminate Regularity and Discriminate Number tasks. In the Discriminate

Regularity group, posterior ERD was more pronounced over the right hemisphere (Figure 3A, B). For the Discriminate Number task, there was no such lateralization (Figure 3C, D). The same effects are shown in Time Frequency plots in Figure 4.

We explored these effects with mixed ANOVA. There was no main effect of Hemisphere, $F(1, 38) = 2.045$, $p = 0.161$, but a significant Hemisphere \times Task interaction, $F(1, 38) = 5.076$, $p = 0.030$, partial $\eta^2 = 0.118$. This confirms the patterns shown in Figures 3 and 4. When people discriminated regularity there was greater desynchronization in the right hemisphere than the left, $F(1, 19) = 4.632$, $p = 0.044$, partial $\eta^2 = 0.196$. Conversely, when people discriminated number, there was no such lateralization, $F(1, 19) < 1$, n.s.

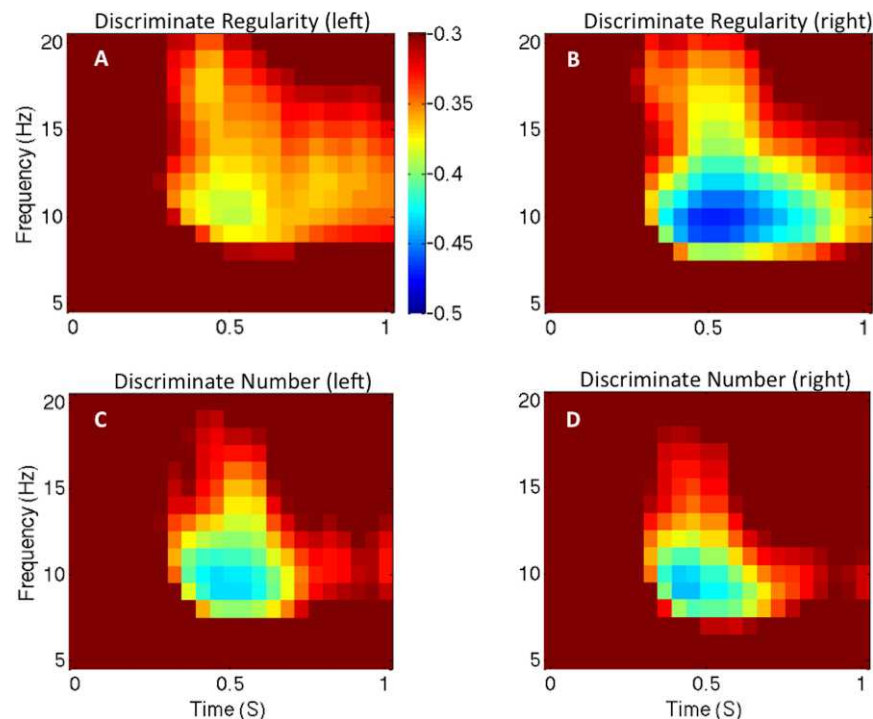


Figure 4. Time-frequency plots. TF plots code power on the colour axis from 5 to 20 Hz, in 50-ms increments. The scale has been chosen to highlight posterior ERD in the 8–13 Hz band, which was used in this analysis. These plots average over regularity and number conditions.

There was no main effect of Regularity, $F(1, 38) < 1$, n.s., or Regularity \times Task interaction, $F(1, 38) < 1$, n.s. However, there was a main effect of Objecthood, $F(1, 38) = 13.348$, $p = 0.001$, partial $\eta^2 = 0.260$, which did not differ between Tasks, $F(1, 38) < 1$, n.s. The effect of Objecthood can be seen in Figure 5. Unlike the relatively transient right lateralization in the Discriminate Regularity task (Figures 3 and 4), there was more

ERD in the two-object condition for a prolonged period, at least up to 1500 ms. We thus reanalyzed this effect with a more appropriate, longer window of 400 to 1500 ms. The main effect of objecthood was now slightly stronger, $F(1, 38) = 18.932$, $p < 0.001$, partial $\eta^2 = 0.333$, and there was still no interaction between Objecthood and Task, $F(1, 38) < 1$, n.s., suggesting that effect of Objecthood on posterior ERD is not

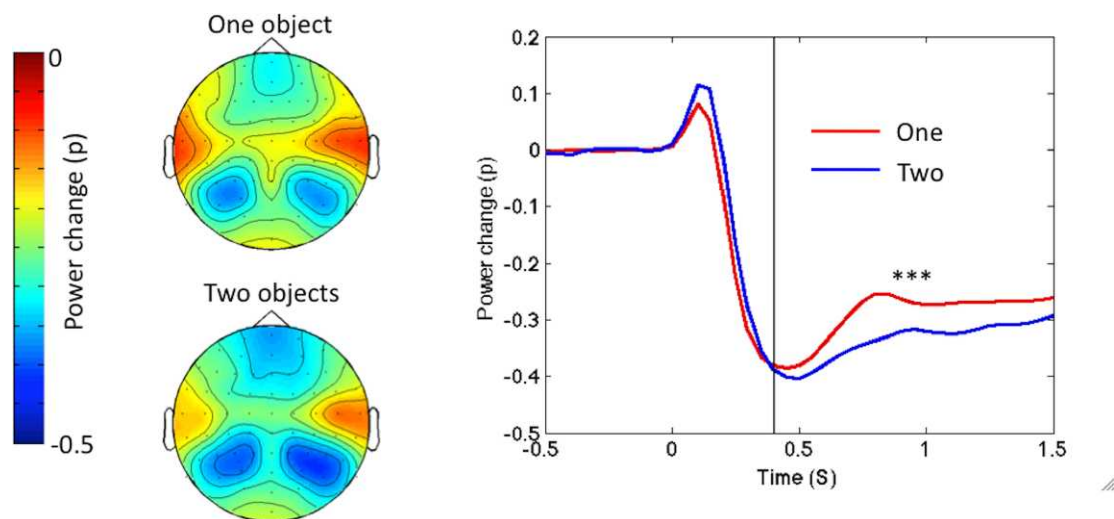


Figure 5. Alpha desynchronization for one and two objects. ERD is shown in the one- and two-object trials. Conventions are the same as Figure 3, except the time window for the topographic plots extends from 400 to 1500 ms. These plots average over task and regularity conditions.

dependent on the participants actively discriminating number of objects.

Despite our predictions, there was no Regularity \times Objecthood interaction, $F(1, 38) < 1$, n.s. There was a Regularity \times Objecthood \times Task interaction, $F(1, 38) = 4.424$, $p = 0.042$, partial $\eta^2 = 0.104$, although there were no significant interactions between Regularity and Objecthood when the Tasks were analyzed separately (Discriminate Regularity [$F(1, 19) = 1.659$, $p = 0.213$]; Discriminate Number [$F(1, 19) = 2.769$, $p = 0.113$]), so this is difficult to interpret. There were no other interaction effects (largest [$F(1, 38) = 1.085$, $p = 0.304$]).

Discussion

In this study we analyzed two EEG signals recorded when participants viewed symmetrical contours that formed closed objects or gaps. It is known that the relative salience of reflection and translation are modulated by contour ownership. In particular, reflectional symmetry is most salient when it is a property of a single object, even for novel abstract shapes. This is not the case for translation, which is more salient as a gap between objects.

There has been much debate about the cause of the Regularity \times Objecthood interaction found in speeded discrimination tasks. It is likely that attention is automatically attracted to objects, so it is easier to discriminate the properties of single objects than gaps between objects (Watson & Kramer, 1999). When translational symmetry is presented, some additional perceptual process may counteract the ubiquitous single object advantage. It could be that translation is discovered through an active *lock and key* matching process, whereby the contours are mentally shifted until they overlap. It is putatively easier to mentally shift the contours when they are properties of separate objects (Baylis & Driver, 1995; Bertamini et al., 1997). However, some evidence conflicts with the lock and key hypothesis and other explanations have also been proposed (Bertamini, 2010; Bertamini, Friedenber, & Argyle, 2002; Koning & Wagemans, 2009).

We searched for an electrophysiological signal that would index the Regularity \times Objecthood interaction, with the hope of shedding light on this phenomenon. Interestingly, there was no comparable interaction effect on the N1 component, which has been shown to be independently sensitive to symmetry (Makin et al., 2013) and perceptual organization (Machilsen et al., 2011). There was also no interaction on another symmetry-related ERP component, the Sustained Posterior Negativity, occurring between 250 and 1000 ms, or in the posterior alpha ERD between 400 and 700 ms. Therefore, the integration of regularity and

objecthood information is not inevitable, and both kinds of information are processed independently at some stages.

Another objective was to identify electrophysiological measures that are purely related to stimulus characteristics. These measures should be independent of the task participants are engaged with. The SPN was fitted this description: It was comparable when people were discriminating regularity and when they were discriminating the number of objects. These results characterize the SPN generators as a bottom-up response to visual symmetry, which is not sensitive to other influences. Note that the SPN was quite small in this study because we are comparing two kinds of regularity. We predict that a study with an equivalent random condition would yield a large SPN for both reflection and translation compared to random (as found in Makin et al., 2013).

The absence of an interaction effect on SPN amplitude is particularly interesting because the SPN *does* systematically relate to other psychophysical findings. Makin et al. (2013) found a clear relationship between SPN amplitude and discrimination speed for different regularities. It was concluded that discrimination speed directly arises from regularity sensitive networks that generate the SPN, and that reflection is the preferred stimulus for these networks. However, it seems the regularity by objecthood interaction in psychophysical studies cannot be related to SPN generators in this way.

The absent interaction is also surprising in light of theoretical work on the role of reflectional symmetry scene segmentation. For example, Pizlo and Stevenson (1999) point out that there are near infinite possible interpretations of two-dimensional retinal images, but the visual system uses prior constraints to discard most of them. It could be that reflectional symmetry is a reliable indicator for a single object, and sensitivity to reflection thus helps with figure-ground segmentation. However, if reflection detection were so intimately linked to single-object discrimination, we would expect different ERPs when reflection is the property of a single object than a gap between two objects; we found no such effect in our symmetry-related ERPs.

Which brain regions generated the SPN? Makin, Wilton, et al. (2012) suggested that the SPN could be the ERP correlate of symmetry-related LOC activations discovered by fMRI methods (Chen et al., 2007; Sasaki et al., 2005; Tyler et al., 2005). In light of the current results, we predict that the fMRI response to symmetry in the LOC would be independent of figural grouping. Indeed, the existing work has reported LOC activations produced by whole field symmetry rather than outline symmetry, which implies some independence from objecthood.

Alpha ERD dissociated from SPN. This component was sensitive to experimental manipulations, but *in a fundamentally different way to the SPN*. The most important effect was that ERD was more pronounced over the right hemisphere, but only in the group of participants who were engaged in regularity discrimination. This differs from the SPN, which was insensitive to task instructions. Another difference was that the Alpha ERD also began later than the SPN. However, ERD was not modulated by regularity, and it did not display the Regularity \times Objecthood interaction. In an earlier study, Makin, Wilton, et al. (2012) found similar, right-lateralized alpha ERD when people compared reflection and random patterns. In most conditions of that study, ERD did not depend on which type of pattern was presented. The current work broadly replicates these results, showing that right ERD is not tuned to stimulus properties, but results from general engagement with the regularity discrimination task. It can be concluded that SPN and right alpha ERD index two distinct stages of visual symmetry discrimination, with quite different profiles. However, neither process uniquely explains the regularity by objecthood interaction found in speeded discrimination tasks.

Although the one- and two-object displays were quite similar (Figure 1), it is clear that participants were sensitive to this manipulation. Amplitude at posterior electrodes was more negative in the two-object condition from the N1 component onwards. Meanwhile bilateral alpha ERD was greater in two-object trials from around 400 ms (Figure 5). These main effects of objecthood were both very robust, and were still clearly present in the group of participants who were discriminating regularity. There is no doubt that the participants were processing the difference between one- and two-object images. However, this did not interact with differential processing of reflection and translation.

Although we can draw no firm conclusions, we may ask which brain areas were responsible for our right-lateralized alpha ERD. Buzsáki (2006) summarizes previous findings, and suggests that the occipital alpha oscillation results from sequences of excitation and inhibition in the long loops connecting early visual regions to the thalamus (see also Pfurtscheller & Lopes da Silva, 1999). This implies that when we record posterior alpha ERD, we record a change in the dominant frequencies of activity in early visual areas. In this case, right-sided ERD suggests greater inputs from the *left* visual field during symmetry discrimination, but not during number discrimination. However, there is no a priori reason to believe symmetry discrimination involves selective attention to inputs from the left side of space, so we do not make strong

claims about the brain regions that generated our scalp ERD.

Conclusions

We have shown that the SPN and right alpha ERD reflect two distinct aspects of symmetry processing in the human brain. However, neither process can explain the regularity by objecthood interaction that is reliably recorded in speeded discrimination experiments. This is intriguing, because the SPN has been clearly shown to reflect other psychophysical findings, including the fact that reflectional symmetry is more salient than other regularities. It is also noteworthy that the SPN and alpha ERD both showed sensitivity to objecthood. We thus conclude that there must be neural processes that are independently sensitive to regularity and objecthood, and that these can be recorded by EEG techniques. Other processes must be responsible for combining these signals, but these do not show up in our scalp recordings. These results are unexpected in the light of previous research, which has suggested that regularity and contour ownership may always be intimately connected (Bertamini et al., 1997; Pizlo & Stevenson, 1999).

We finish by noting that neural independence of symmetry and objecthood is entirely consistent with models of symmetry perception inspired by whole-field symmetry, where the issue of figure and ground does not arise. For example, Barlow and Reeves (1979) measured symmetry discrimination in dot-clouds, and proposed that the visual system checks for equivalent dot density in matched regions on either side of the axis. This model says nothing about the consequences of dots falling in separate figure or ground areas, and allows for the possibility that symmetry detection is independent from other perceptual groupings afforded by the same image. More generally, it is often important to recognize highly asymmetrical objects (e.g., rocks on a path), and possible to perceive regular layouts of multiple objects that span figure and ground regions (e.g., cars in a car park). Perhaps obligatory, low-level interaction between symmetry and objecthood would mislead us *too often*, so these features are processed independently.

Keywords: symmetry, reflection, translation, ERPs, alpha desynchronization

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